# ON THE OSMOTIC CONCENTRATION OF THE TISSUE FLUIDS OF DESERT LORANTHACEAE*

By J. Arthur Harris

*Station for Experimental Evolution*

## I. Introductory remarks

In an earlier publication Mr. Lawrence and I† discussed a series of determinations of the osmotic concentration of the tissue fluids of Jamaican montane rain-forest Loranthaceae parasitic on various hosts. The purpose of this paper is to present the results of studies of the sap concentration of the tissue fluids of desert mistletoes and of that of their host plants for comparison with the rain-forest series already published.

The number of determinations upon which the conclusions of the present paper is based is not so large as that which Mr. Lawrence and I were able to obtain in Jamaica. In explanation I may merely say that the difficulties under which the desert series was secured were far greater‡ than those which surrounded the work in the Blue Mountains. This has necessarily restricted the number of determinations, and notwithstanding our best

* Coöperative investigations carried out under the auspices of the Department of Botanical Research and the Department of Experimental Evolution, of the Carnegie Institution of Washington.

I am greatly indebted to Mr. P. C. Standley, of the United States National Herbarium, for identifying these and other Arizona plants. Dr. Trelease, whose splendid monograph of the genus *Phoradendron* has recently appeared, has kindly gone over the parasites.

† Harris, J. Arthur, & Lawrence, John V. On the osmotic pressure of the tissue fluids of Jamaican Loranthaceae parasitic on various hosts. Am. Jour. Bot. **3**: 438–455. 1916.

‡ I am greatly indebted to the director and the staff of the Desert Laboratory for every facility that could be given for these studies. The difficulties were such as are inseparable from physiological work in camp under summer conditions in the Southwestern deserts. For example, the torrential rains, which are characteristic of the region during the midsummer season, more than once cut us off from supplies or facilities necessary for our work.

efforts has possibly limited somewhat the precision of the determinations.*

While I hope later to secure larger, and better, series of data on osmotic concentration in the tissue fluids of desert Loranthaceae, and to obtain series from mesophytic regions for comparison with those from the hygrophytic and xerophytic habitats now available, there is little prospect of the completion of this work in the near future. It seems proper, therefore, to place on record the results so far obtained on the desert species for the use of other physiologists.

In the present state of our knowledge, determinations of the properties of the tissue fluids of desert Loranthaceae have a two-fold interest.

1. In studies in the Arizona† and the Jamaican coastal deserts,‡ my associates and I have confirmed the conclusions of Drabble and Drabble and of Fitting by showing that the osmotic concentration of the sap of desert plants is in general far higher than that of those of mesophytic and hygrophytic regions. It seems a matter of considerable interest to determine whether the same relationship holds for the Loranthaceae of these climatically antithetical regions.

2. In our first study we found that the concentration of the tissue fluids of the parasite is generally, but not invariably, higher than that of the host plant. It seems desirable to test this

* Because of the rapid evaporation in the desert air, the danger of differential water loss in the collection of the tissues of parasite and host was far greater in the desert series. Because of the higher temperature to which the tubes of tissue were necessarily subjected until they could be placed in the freezing mixture, the danger of changes in the composition of the sap were necessarily greater than in the cool climate of the Blue Mountains. The concentrations in molecules and ions of the solutes, not the nature of the constituent compounds which may possibly be somewhat altered, is the subject under investigation. It may be doubted whether standing even for a much longer time would seriously alter concentration. Furthermore, any changes of this kind would be quite as likely to affect the tissues of both host and parasite, and hence to leave the relationship between them unaltered, as to influence one alone.

† Harris, J. Arthur, & Lawrence, John V., with the coöperation of Gortner, R. A. The cryoscopic constants of expressed vegetable saps as related to local environmental conditions in the Arizona deserts. Phys. Res. **2**: 1–49. 1916.

‡ Harris, J. Arthur, & Lawrence, John V. Cryoscopic determinations on tissue fluids of plants of Jamaican coastal deserts. Bot. Gaz. **64**: 285–305. 1917.

conclusion against data from as widely dissimilar environmental conditions as possible.

## II. Presentation of data

Since earlier studies have shown that in trees the concentration of leap sap is related to the height of insertion of the leaves,* care was taken in the collection of samples of the host leaves to secure them from as nearly as possible the same level as the parasite. Generally they were gathered from the same branch.

Osmotic concentration was measured by the cryoscopic method. Sap was extracted after freezing† the tissues to obviate the differential extraction of sap, first carefully investigated by Dixon and Atkins‡ and verified by ourselves.§

The results are expressed in terms of freezing-point lowering in degrees centigrade, corrected for undercooling‖ and in atmospheres pressure from a published table.¶

The actual constants for parasite and host, together with the habitats of the species and the dates of the determinations, are given below.

The original collection numbers are retained. The values at the extreme right are the constants for the parasites. Below these are given the differences between the concentrations of parasite and host, the positive sign indicating higher and the negative sign indicating lower osmotic concentration in the tissue fluid of the parasite.

* Harris, J. Arthur, Gortner, R. A., & Lawrence, J. V. The relationship between the osmotic concentration of leaf sap and height of leaf insertion in trees. Bull. Torrey Club **44**: 267–286. 1917.

† Gortner, R. A., & Harris, J. Arthur. Notes on the technique of the determination of the depression of the freezing point. Plant World **17**: 49–53. 1914.

‡ Dixon, H. H., & Atkins, W. R. G. Osmotic pressures in plants. I. Methods of extracting sap from plant organs. Sci. Proc. Roy. Dublin Soc. N. S. **13**: 422–433. 1913. Also in Notes from Bot. Sch. Trin. Coll. Dublin **2**: 154–172. 1913.

§ Gortner, R. A., Lawrence, John V., & Harris, J. Arthur. The extraction of sap from plant tissues by pressure. Biochem. Bull. **5**: 139–142. *pl. 1.* 1916.

‖ Harris, J. Arthur, & Gortner, R. A. Note on the calculation of the osmotic pressure of expressed vegetable saps from the depression of the freezing point, with a table for the values of $P$ for $\Delta = .001°$ to $\Delta = 2.999°$. Am. Jour. Bot. **1**: 75–78. 1914.

¶ Harris, J. Arthur. An extension to 5.99° of tables to determine the osmotic pressure of expressed vegetable saps from the depression of the freezing point. Am. Jour. Bot. **2**: 418–419. 1915.

In several cases more than one mistletoe was taken from the same host tree. In such cases determinations based on the sap of the individual parasites may be compared with a single constant for the host plant, or may be compared with the determination based on the sample of host leaves nearest the parasite. Differences which for some reason indicated by the context are regarded as of doubtful value are bracketed.

*Phoradendron californicum* Nutt.

Coll. 531, on *Acacia Greggii* Gray. Aug. 12.

$\Delta = 2.00$, P = 24.0

For host, $\Delta = 1.87$, P = 22.5 $+0.13$, $+1.5$

On sandy floor of Sabino Creek, near mouth of Sabino Canyon, Santa Catalina Mountains.

Coll. 546, on same species, Aug. 15. $\Delta = 1.82$, P = 21.8

For host, $\Delta = 1.68$, P = 20.2 $+0.14$, $+1.6$

Small arroyo on bajada between Tucson and Sabino Canyon, Santa Catalina Mountains.

Coll. 535, on *Cercidium Torreyanum* (S. Wats.) Sarg. Aug. 13.

$\Delta = 1.99$, P = 23.9

For host, $\Delta = 1.55$, P = 18.7 $+0.44$, $+5.2$

Coll. 574, on same species, Aug. 19. $\Delta = 2.45$, P = 29.4

No determination for host.

The first of these collections from *Cercidium* was taken in the same locality as the August 15 sample from *A. Greggii*. The second was taken from a very small shrub in Sabino Canyon, on a steep slope about two or three miles below Dam Site. The lack of daylight precluded a collection of the very small leaves of the host.

Coll. 267, on *Prosopis velutina* Wooton, July 6.

$\Delta = 2.65$, P = 31.8

For host, $\Delta = 2.64$, P = 31.6 $+0.01$, $+0.2$

Coll. 538, on same species, Aug. 14. $\Delta = 2.29$, P = 27.5

For host, $\Delta = 2.40$, P = 28.8 $-0.11$, $-1.3$

These two collections were from the same large mesquite tree, on the edge of a small arroyo on the upper bajada, near the mouth of Sabino Canyon. The first collection was taken before the earlier summer rains, the second after they had fallen. The samples of parasites were from different plants.

*Phoradendron Coryae* Trel., on *Quercus*

Dr. Trelease notes that certain of these numbers belong in his form *stenophylla*, but it has not seemed worth while for present purposes to separate these from the more typical *P. Coryae.*

As far as known this species occurs exclusively on *Quercus*. The leaves of these desert oaks are so hard that at the mid-summer season when these determinations were made it was impossible to express sufficient sap from them to make freezing-point determinations.

On *Quercus oblongifolia* Torr.

| | | |
|---|---|---|
| Coll. 282, | Mistletoe 1, | $\Delta = 2.23$, $P = 26.7$ |
| | Mistletoe 2, | $\Delta = 2.09$, $P = 25.1$ |
| Coll. 283, | Mistletoe 1, | $\Delta = 2.01$, $P = 24.2$ |
| | Mistletoe 2, | $\Delta = 1.88$, $P = 22.6$ |

All four determinations were made on samples collected July 10 on two trees in the Basin, Santa Catalina Mountains.

Coll. 292, on *Quercus Emoryi* Torr. $\Delta = 2.15$, $P = 25.9$

The Basin, Santa Catalina Mountains, July 11.

Coll. 528, on *Quercus hypoleuca* Engelm. August 10.

$\Delta = 1.73$, $P = 20.8$

Coll. 570, August 19. $\Delta = 2.26$, $P = 27.1$

Both of these collections were taken from a very large *Phoradendron* on a small oak, growing among the boulders on the edge of Sabino Creek, in the Basin, Santa Catalina Mountains. The first determination seemed suspiciously low, and the second sample was taken from the same individual plant on the 19th to check the results.

Coll. 355, on *Quercus arizonica* Sarg. July 19.

$\Delta = 2.63$, $P = 31.5$

Near Mud Springs, Santa Catalina Mountains.

Coll. 356, on same species July 20. $\Delta = 2.43$, $P = 29.1$

On Mount Lemmon trail, between the Basin and Mud Springs.

*Phoradendron macrophyllum* (Engelm.) Cockerell on *Fraxinus attenuata* Jones

For the host and parasite I am able to give determinations made in the early spring of 1914 and in the summer of 1916. The results secured on the desert mistletoe in the early spring of

1914 suggested the desirability of the later studies in Jamaica and Arizona.

The spring determinations were made from trees in the sandy (generally dry) bed of Agua Verde Creek, Tanque Verde Mountains.

| | | |
|---|---|---|
| Coll. 94, Mar. 24, 1914. | | $\Delta = 2.56$, P = 30.7 |
| | For host, $\Delta = 1.39$, P = 16.7 | + 1.17, + 14.0 |

The leaves of the host had not yet attained their full size. The leaves of the parasite, which was in flower, were of course old. A second visit to this locality was made later to determine whether the striking difference in the sap of the two sets of leaves might be due merely to differences in maturity. On April 8 the still not fully matured leaves of the host gave $\Delta = 1.44$, P = 17.3, agreeing well with the values obtained on our first visit.

| | | |
|---|---|---|
| Coll. 171, April 9, 1914. | | $\Delta = 2.28$, P = 27.4 |
| | For host, $\Delta = 1.63$, P = 19.6 | + 0.65, + 7.8 |

These values, from a second large tree in the same locality, are in excellent agreement with those cited above.

The following determinations were made on samples collected along Sabino Creek, at the mouth of Sabino Canyon, Santa Catalina Mountains.

| | | |
|---|---|---|
| Coll. 268, July 7, 1916. | | $\Delta = 3.29$, P = 39.5 |
| | For host, $\Delta = 2.08$, P = 24.9 | + 1.21, + 14.6 |
| Coll. 270, July 7, 1916. | | $\Delta = 2.46$, P = 29.5 |
| | For host, $\Delta = 1.90$, P = 22.8 | + 0.56, + 6.7 |

The first of these samples was taken from a single large mistletoe, the second from a number of small plants on another tree.

Coll. 576, August 19, 1916.

| | |
|---|---|
| Sample B, | $\Delta = 1.96$, P = 23.6 |
| | − .29, − 3.4 |
| Sample C, | $\Delta = 2.33$, P = 28.0 |
| | + 0.08, + 1.0 |
| Sample D, | $\Delta = 2.53$, P = 30.4 |
| | + 0.28, + 3.4 |
| Sample E, | $\Delta = 2.69$, P = 32.3 |
| | + .44, + 5.3 |

All these were taken from the same small host tree, with injured trunk and several dead limbs, but with the living parts apparently in a perfect'y healthy and vigorous condition. The sap from the leaves of the host gave $\Delta = 2.25$, $P = 27.0$.

I was able to find only two trees of *Fraxinus* with *Phoradendron* in the Basin, Santa Catalina Mountains. The results are:

| | |
|---|---|
| Coll. 518, Aug. 9. | $\Delta = 1.97$, $P = 23.7$ |
| For host, $\Delta = 1.58$, $P = 19.0$ | $+0.39$, $+\ 4.7$ |
| Coll. 520, Aug. 9. | $\Delta = 2.15$, $P = 25.8$ |
| For host [$\Delta = 3.23$, $P = 38.7$] | —— —— |
| For host, Aug. 19, $\Delta = 2.15$, $P = 25.9$ | |
| | [$\pm 0$, $-\ 0.1$] |

The two collections of the parasite made on August 9 are very consistent. The determination for the host in the case of the second is obviously erroneous, presumably because of contamination with salt. On August 19 another trip was made to the Basin for the specific purpose of obtaining another collection from this tree. The determination based on a sample of that date gives a distinctly lower value than the first determination from this tree, but a higher value than the one obtained August 9 from the first tree. Unfortunately there was not enough of the parasite for a second collection.

### *Phoradendron macrophyllum Jonesii* Trel. on *Fraxinus attenuata* Jones

The following determinations were made from collections along Sabino Creek, at the mouth of Sabino Canyon, Santa Catalina Mountains.

| | |
|---|---|
| Coll. 542, August 14, First Mistletoe | $\Delta = 1.99$, $P = 23.9$ |
| For host, $\Delta = 2.17$, $P = 26.1$ | $-0.18$, $-\ 2.2$ |
| Second Mistletoe | $\Delta = 1.94$, $P = 23.4$ |
| Same host determination | $-0.23$, $-\ 2.7$ |

My notes state in regard to the first of these parasites that the leaves are very yellow. Note that in both cases the determination for the parasite is lower than is usually the case.

| | |
|---|---|
| Coll. 575, August 19, 1916. | $\Delta = 2.51$, $P = 30.1$ |
| For host, $\Delta = 1.79$, $P = 21.5$ | $+\ .72$, $+\ 8.6$ |
| August 19, 1916. | $\Delta = 2.54$, $P = 30.5$ |
| Same host tree, $\Delta = 1.76$, $P = 21.1$ | $+0.78$, $+\ 9.4$ |

Two collections of leaves from the same host tree were made. The results are in excellent agreement.

*Phoradendron macrophyllum* on *Populus*

Four determinations on *Populus Wislizenii* (S. Wats.) Sarg. were secured from two large trees, 4–5 feet in diameter, on the banks of the Rio Rillito, August 12.

| | |
|---|---|
| Coll. 532, Parasite 1, | $\Delta = 1.96$, $P = 23.6$ |
| | $+ 0.35$, $+ 4.3$ |
| Parasite 2, | $\Delta = 1.91$, $P = 22.9$ |
| | $+ 0.30$, $+ 3.6$ |

For host, $\Delta = 1.61$, $P = 19.3$

The leaves of the host were taken as near as possible to Parasite 1.

| | |
|---|---|
| Coll. 533, Parasite 1, | $\Delta = 1.94$, $P = 23.3$ |
| For host, $\Delta = 1.79$, $P = 21.5$ | $+ 0.15$, $+ 1.8$ |
| Parasite 2, | $\Delta = 2.13$, $P = 25.6$ |
| For host, $\Delta = 1.76$, $P = 21.2$ | $+ 0.37$, $+ 4.4$ |

The two samples of the leaves of the host were taken as near as possible to the parasites with which they are compared.

## III. DISCUSSION OF CONSTANTS

Taking the results for the broad-leaved *Phoradendron*, *P. macrophyllum* and *P. macrophyllum Jonesii*, on *Fraxinus*, the data show that in both of the two determinations made in the early spring the osmotic concentration of the tissue fluids of the parasite was considerably higher than that of its host plant.

The average of the two determinations is 29.05 atmospheres for the parasite as compared with 18.15 atmospheres for the host, or an average difference of 10.90 atmospheres.

In the summer collections, the data show that there are eight cases in which the osmotic concentration of the parasite is higher than that of the host as compared with three cases in which it is lower.*

* The results for one determination (Coll. 520) are not included because the only trustworthy value for the host was obtained on a different date. Two of these determinations (Coll. 542) are based on two different parasites on the same tree, with only one determination of the best plant for comparison. In one case the leaves of the parasite were definitely noted as old. The third exception (Coll. 576) came in a series in which four samples were taken from a partly dead tree. Possibly this one of the four plants was not in a normal condition.

The average freezing-point lowering of the tissue fluids of the parasite is 2.383° as compared with 2.041° in the fluids of the host, or a difference of + .342°.

In terms of osmotic pressure, the average for the sap of the parasite is 28.63 atmospheres, that of the host is 24.50 atmospheres, and the average difference between them is + 4.13 atmospheres.

The four determinations of *P. macrophyllum* on *Populus* are consistent in indicating higher osmotic concentration in the parasite. The excess ranges, roughly, from 1 to 5 atmospheres. The average for the four comparisons is 23.85 atmospheres for the parasite and 20.33 atmospheres for the host, a difference of 3.52 atmospheres.

Thus there are for the leafy desert Loranthaceae 14 determinations in which the concentration of the parasite exceeds that of the host against three cases in which the reverse is true.

Of the five determinations based on *P. californicum* in which comparison with the host is possible, four show an excess for the parasite, but the difference is extremely slight in one case. Far more work must be done before any final conclusions can be drawn concerning the relationship of the sap concentration of parasite and host in the leafless forms.

## IV. RECAPITULATION

This paper presents data toward the solution of the problem of the water relationships of the desert Loranthaceae.

Three species of the genus *Phoradendron*, the leafless *P. californicum* and the leafy *P. Coryae* and *P. macrophyllum*, have been investigated on a number of hosts.

The osmotic concentration of the tissue fluids of the Loranthaceae of the Arizona deserts is, roughly speaking, twice as great as demonstrated by similar methods in the tissue fluids of the species investigated in the montane rain-forest of the Jamaican Blue Mountains.

In desert Loranthaceae, as in those of the montane rain-forest, the osmotic concentration of the tissue fluids of the parasite is generally, but not invariably, higher than that of the host.

These studies will be continued.